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THE REORGANIZATION OF THE DORYLOCERUS COMPLEX BY THE USE OF NUMERICAL ANALYSIS WITH SOME NEW DISTRIBUTION RECORDS AND NEW DATA ON THEIR BEHAVIOR (COLEOPTERA, STAPHYLINIDAE)[1]

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ABSTRACT

The Dorylocerus complex is herewith reorganized and the generic name Dorylopora synonymized. A new key to the genera of the Dorylocerus complex is provided with the newly included Dorylobius Raffray. The genus Draconula is redescribed and a new species D. decellei (Zaire) included. A new species, Dorylocerus carinata (Zambia), is described. The species groups of Dorylocerus are reorganized following results of numerical analyses. The food habits and social biology of the Dorylocerus is reviewed and evolutionary trends are discussed.

INTRODUCTION

The tribe Deremini is 1 of the most difficult tribes of the Aleocharinae. All of the species are small and it has been difficult to establish generic limits and definitions within the various groups. The first revisions of parts of the tribe (Kistner 1966, 1968a) which were the first revisions ever attempted, cut out what were thought to be the most distinctive and closely related genera and combined them into what was then called the Dorylopora complex. This complex contained the genera Dorylopora Wasmann, Dorylocerus Wasmann, Rodylopora Kistner, Draconula Kistner, and Fossulopora Kistner. In order to be included in the Dorylopora complex, species needed to have longitudinal grooves or furrows in the head, pronotum, and elytra collectively. That arrangement of the species in the genera is shown in Table 1.

Since those revisions, numerous new specimens of the complex have been

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Table 1. Organization of the Dorylopora Complex (after Kistner)

Species number	Species	Species group (if defined)
1	Dorylopora costata Wasmann	costata
2	Dorylopora fletcheri Kistner	
3	Dorylopora pseudocostata Kistner	
4	Dorylopora afer Kistner	kohli
5	Dorylopora kohli Wasmann	
6	Dorylopora morio Kistner	
7	Dorylopora nigra Kistner	
8	Dorylopora abdominalis Cameron	abdominalis
9	Dorylopora carlislei Kistner	
10	Dorylopora congolensis Kistner	congolensis
11	Dorylopora ivoiriensis Kistner	
12	Dorylopora excisicollis Cameron	excisicollis
13	Dorylopora solea Kistner	
14	Dorylopora alzadae Kistner	alzadae
15	Dorylopora kalongeana Kistner	
16	Dorylopora minor Eichelbaum	
17	Dorylocerus fossulatus Wasmann	----
18	Rodylopora attenuata Kistner	----
19	Fossulopora camerounicus Kistner	----
20	Fossulopora congoensis Kistner	
21	Fossulopora orientalis Kistner	
22	Draconula minuta Kistner	----

collected including 2 new species, 1 in the genus Draconula and another in the genus Dorylocerus. The new species in Dorylocerus proved to have a campanulate pronotum which knocked out the most important character which formerly separated the genera Dorylocerus and Dorylopora. It was therefore decided to reexamine the relationships of all the species using numerical methods. The purpose of this paper then is to present the results of these analyses, to redescribe the genus Dorylocerus and synonymize the genus Dorylopora, to redescribe the genus Draconula (made necessary by the inclusion of a new species), and to redefine some of the species groups.

Since the last revision another genus, Dorylobius Raffray has been shown to be a member of this complex and while there is not sufficient material to dissect specimens for the numerical analyses, it will be included in the new generic key and illustrated.

METHODS AND MATERIALS

A. Characters. The species characters chosen for the numerical analysis were all checked against the specimens and the published descriptions. The list of 63 characters given in Table 2 was developed according to the general plan outlined by Sokal and Sneath (1963). Characters were chosen which could be scored as either present (1), absent (0), or no comparison (3).

In many instances, a character was coded easily where a structure was present in some species and absent in others. But where a structure was present in all 24 species, a character could be developed around the structure by further defining it qualitatively. Character 6, "head with a well-defined longitudinal median groove," is an example of this. The presence of this groove in the head is 1 of the diagnostic characteristics of the complex, and yet we find

Table 2. The basic set of sixty-three characters used to compare the species of the Dorylocerus complex.

1. Dorsal surface of head, pronotum, and elytra punctate
2. Dorsal surface of head, pronotum, and elytra with yellow setae
3. Dorsal surface of head, pronotum, and elytra with tubercles
4. Head length and width about equal
5. Head with a well-defined longitudinal median groove
6. Head with 2 lateral grooves
7. Anterior border of vertex delineated by a carina
8. Head with 2 raised longitudinal carinas
9. Head with 4 raised longitudinal carinas
10. Head with 2 posteriorly directed projections
11. Neck well-defined.
12. Pronotum length less than 0. 32 mm
13. Pronotum length greater than 0. 32 mm but less than 0. 42 mm
14. Pronotum length greater than 0. 42 mm
15. Pronotum campanulate
16. Pronotum subquadrate
17. Lateral borders of pronotum notched or indented
18. Pronotum with a longitudinal median groove
19. Pronotum with lateral grooves
20. Pronotum with carina(s)
21. Pronotum with many chitinous projections
22. Prosternum with a well-developed median carina
23. Mesosternum shorter than metasternum
24. Intercoxal process of mesosternum carinate
25. Elytra length less than 0. 27 mm
26. Elytra length greater than 0. 27 mm but less than 0. 35 mm
27. Elytra length greater than 0. 35 mm
28. Elytra with well-defined medial ridges and with a depressed region between them
29. Elytra with well-defined lateral ridges and with a depressed region between them
30. Elytra with 3 ridges each
31. Abdominal spiracles greatly enlarged
32. Posterior border of abdominal tergite II notched
33. Posterior border of abdominal tergite III notched
34. Posterior border of abdominal tergite IV notched
35. Posterior border of abdominal tergite V notched
36. Posterior border of abdominal tergite VI notched
37. Posterior border of abdominal tergite III indented but not notched
38. Posterior border of abdominal tergite IV indented but not notched
39. Posterior border of abdominal tergite V indented but not notched
40. Posterior border of abdominal tergite VI indented but not notched
41. Posterior border of abdominal tergite VII indented but not notched
42. Posterior border of abdominal tergite II with 2 blunt projections
43. Posterior border of abdominal tergite III with 2 blunt projections
44. Posterior border of abdominal tergite IV with 2 blunt projections
45. Posterior border of abdominal tergite V with 2 blunt projections
46. Posterior border of abdominal tergite VI with 2 blunt projections
47. Abdominal tergite II with macrochaetae
48. Abdominal tergite III with macrochaetae
49. Abdominal tergite IV with macrochaetae
50. Abdominal tergite V with macrochaetae
51. Abdominal tergite VI with macrochaetae
52. Abdominal tergite VII with macrochaetae
53. Sternite III with raised chitinous projections
54. Sternite IV with raised chitinous projections
55. Sternite V with raised chitinous projections
56. Sternite VI with raised chitinous projections
57. Sternite VII with raised chitinous projections

58. Abdominal tergite II with raised areas
59. Abdominal tergite III with raised areas
60. Abdominal tergite IV with raised areas
61. Abdominal tergite V with raised areas
62. Abdominal tergite VI with raised areas
63. Abdominal tergite VII with raised areas

that in Dorylocerus minor the groove is quite pronounced, while in the species of Fossulopora the groove is quite shallow. By stipulating that the groove be well-defined, character 6 thus serves to differentiate these species qualitatively, D. minor being scored 1 for this character and the species of Fossulopora being scored 0.

The pronotum and elytra lengths were examined to determine if these were feasible characters to use, and it was found that the lengths of each were roughly divided into three groups as shown below:

Pronotum	Elytra
pronotum less than 0.32	elytra less than 0.27
pronotum between 0.32 and 0.42	elytra between 0.27 and 0.35
pronotum greater than 0.42	elytra greater than 0.35

To avoid weighting these measurement characters, each species was scored "3" for groups not applicable to that species. All measurements in this paper are in mm unless otherwise stated.

In coding the pronotum lengths, 3 species, Dorylocerus kohli, D. fossulatus, and Rodylopora attenuata, were not in 1 group exclusively and had to be scored "1" in 2 groups. The measurements of D. fossulatus happen to fall exactly on the dividing point. There was no range in this measurement simply because only 1 specimen of the species has ever been found. Four species received a "1" score in 2 measurement groups for elytra length. These were Dorylocerus alzadae, D. kohli, D. pseudocostata, and Rodylopora attenuata. The character coding for each species is given in Table 3.

Kistner (1968b) mentions the use of the beetles' color as a character but notes that this characteristic sometimes does not yield reliable placement of species, probably because of convergence. Because the color differences of these beetles are not clearly distinctive and vary considerably within species, coloration was not used as a character here.

Kistner's revisions of the old Dorylopora complex, include drawings of parts of the male and female genitalia of most of the species. These show that, while some groupings of species could possibly be made on the basis of these structures, the structures are highly individualistic for the species. Thus they serve to separate species more than to show their similarities. Therefore, the shapes of the genitalia were not used for the numerical analyses.

B. Statistical comparison. The data were read into a CDC 3150 computer along with a program to produce the simple matching coefficients described by Sokal and Michener (1958) which were then used to produce a clustering of the species according to the weighted-pair-group method described by Sokal and Sneath (op. cit.). Copies of this program are available upon request.

C. Other methods. To find out what the beetles had eaten, FAA fixed specimens were imbedded in 63-65° C melting point paraffin and sectioned. These sections were stained using a Hematoxylin-Phloxine-Light Green technique or the Matsuo tetrachrome technique. The same sections provided the

Table 3. Character matrix of 24 species of the Dorylocerus complex. Characters are arranged sequentially from left to right.

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          10        20        30        40        50        60
 1 100110000013130101110010313110011100000000000000000000000000
 2 100110010013130101110010313110011111000000000000000000010000
 3 100110000011330101110010113110011000000000000000000000111110
 4 100110000011330101100010133000000000000000000000000000000000
 5 100110000011130101100010113000000000000000000000000000000000
 6 100111000011330101100010133000000000000000000000000000000000
 7 100111000011330101100010313000000000000000000000000000000000
 8 100111111013310101110011331110011111000001111100000000000111110
 9 100111111013130101110011313110011100000011100000000000000111111
10 110110000013130111100010331110000001110000000000000000000000000
11 110100000013310111100010331110000001110000000000000000000000000
12 100111111013130111110111313110011100000011100000000000000111110
13 100111111011330111110111313110011100000011000000000000000111110
14 100111000013130111100010311110011111000001111000000000000011110
15 100111000013310111100010331110011111000001111000000000000011110
16 100111000013130111110010313110011111000001111000000000000001110
17 110100000011131011100001313010100000000000000000000000000000000
18 011000000013111001100010311110100000111000000011111100000000000
19 010100000111330100100010133000011100000000000011110000000000000
20 010100000111330100000010133010001111000000000011111000000011110
21 010100000113130100100010313110011000011110000011110000000011111
22 000010100001330011111110133111011100000001110000011111111111100
23 001010100003130011100110133110011111000001111011111111111111110
24 100011010113131001110111331110011110000101111000000000000111110
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basis for a gland survey.

Observations of behavior were made in the field directly in the ant columns as well as with specimens placed in petri dishes or Wilson ant nests together with their hosts.

RESULTS

Half of the original coefficients of association are shown in Table 4, the other half being a mirror-image of what is shown in the table. The degree of affinity of all the species is represented in the phenogram shown in Fig. 1. The abscissa is the magnitude of the coefficient of association and the actual value is given at each branch in the phenogram. The relationships are the same as those determined by traditional means by Kistner, but there are certain exceptions which follow:

The old genus Dorylopora is synonymous with Dorylocerus. This was obvious to us as soon as the new species D. carinata showed up but it is interesting that the clustering technique put D. fossulatus between the congolensis group and the costata group. The name Dorylocerus has priority by page so all species formerly in the genus Dorylopora are herewith transferred to Dorylocerus. These species are: D. afer, D. kohli, D. morio, D. nigra, D. congolensis, D. ivoiriensis, D. costata, D. fletcheri, D. pseudocostata, D. abdominalis, D. carlislei, D. excisicollis, D. solea, D. alzadae, D. kalon-

geana, and D. minor. The new species of Dorylocerus is distinct and is described below.

Table 4. First matrix of coefficients of relationship for the species of the Dorylocerus complex.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	.932	.897	.895	.898	.877	.879	.702	.763	.845	.825	.746	.759	.797	.789	.831	.780	.644	.789	.649	.661	.579	.466	.672
2		.862	.825	.831	.807	.810	.772	.763	.776	.754	.746	.759	.797	.789	.797	.712	.576	.719	.684	.627	.544	.500	.707
3			.831	.833	.814	.814	.772	.828	.772	.754	.810	.831	.828	.825	.828	.712	.569	.695	.695	.724	.627	.534	.737
4				1.000	.983	.983	.596	.649	.877	.860	.632	.655	.719	.719	.719	.845	.667	.797	.661	.614	.492	.397	.561
5					.983	.983	.596	.661	.879	.860	.644	.661	.729	.719	.729	.850	.678	.797	.661	.627	.492	.407	.569
6						1.000	.614	.667	.860	.842	.649	.672	.737	.737	.737	.828	.649	.780	.644	.596	.475	.379	.579
7							.614	.672	.860	.842	.655	.678	.741	.737	.741	.831	.655	.776	.638	.603	.466	.368	.579
8								.912	.552	.542	.895	.877	.845	.847	.842	.509	.356	.491	.561	.491	.561	.579	.828
9									.603	.579	.949	.931	.831	.825	.831	.576	.407	.544	.544	.593	.614	.534	.810
10										.983	.621	.632	.712	.707	.707	.828	.763	.702	.596	.672	.456	.379	.525
11											.596	.614	.690	.695	.684	.842	.780	.719	.614	.684	.439	.351	.500
12												.983	.847	.842	.847	.593	.390	.526	.526	.542	.667	.586	.828
13													.828	.825	.828	.610	.397	.552	.552	.552	.655	.561	.807
14														1.000	.966	.644	.483	.614	.649	.627	.614	.638	.814
15															.965	.632	.475	.614	.649	.614	.614	.632	.810
16																.644	.475	.614	.614	.593	.614	.603	.810
17																	.729	.707	.603	.576	.431	.345	.552
18																		.702	.632	.678	.421	.483	.424
19																			.831	.789	.458	.466	.491
20																				.789	.458	.569	.526
21																					.404	.466	.534
22																						.810	.596
23																							.586

The new species of Draconula is distinct and is described below. Since the second species is sufficiently different from D. minuta, the only previously known species, it changes the generic concept a bit and so Draconula is redescribed below.

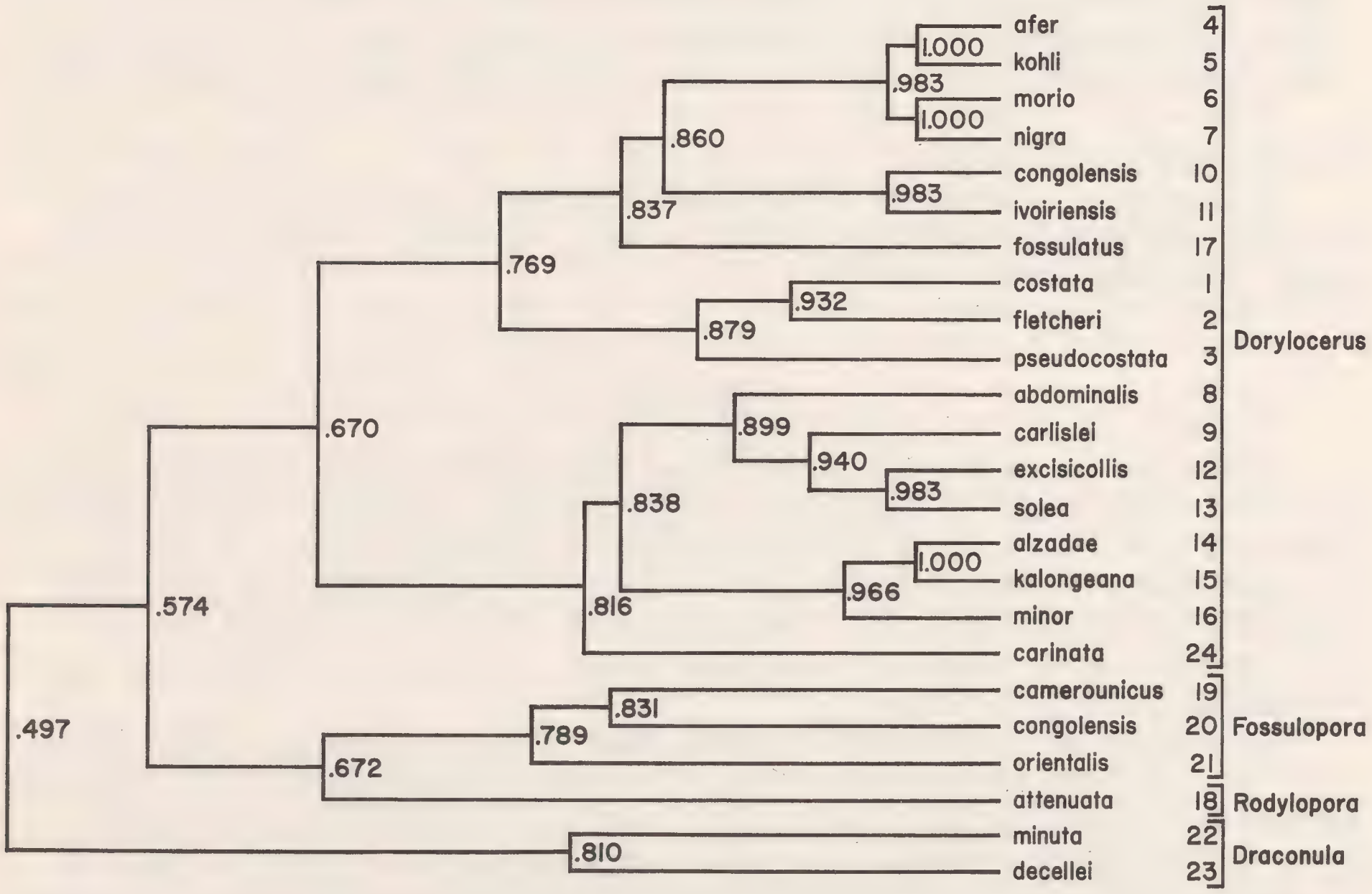

Fig. 1--Phenogram of the genera and species of the Dorylocerus complex.

The abdominalis group of the genus Dorylocerus should be restructured to include the old excisicollis and alzadae groups following the cluster shown in Fig. 1. A key to the new species groups will be included plus a key to all species within each group.

KEY TO GENERA OF THE DORYLOCERUS COMPLEX

1 Head, pronotum, and elytra all with grooves..... 2
Head, pronotum and elytra not all grooved (1 or 2 may be grooved but not all) .....other generic complexes of the tribe Deremini

2 (1) Abdominal tergites II-VII without macrochaetae; dorsal surfaces of the head, pronotum, and elytra punctate..... Dorylocerus
Abdominal tergites II-VII with some macrochaetae; dorsal surfaces of the head, pronotum, and elytra shagreened or smooth and shiny 3

3 (2) Pronotum spindle-shaped, sometimes with lateral projections, always with chitinous projections; sternites and tergites with raised chitinous projections ..... Draconula
Pronotum not spindle-shaped, never with lateral projections; tergites only with raised chitinous projections..... 4

4 (3) Pronotum with a median hole; abdominal spiracles normal in size.....
..... Fossulopora
Pronotum with a median groove; abdominal spiracles greatly enlarged
..... 5

5 (4) Eyes extremely small, located just at base of antennae .....
..... Dorylobius (Fig. 2B)
Eyes of normal size..... Rodylopora

Redescription of the Genus Draconula

Distinguished from all other genera including Rodylopora to which it is most closely related by the unique head and pronotum shape and the unique form of the abdominal macrochaetae.

Head capsule one-fifth to one-half longer than wide, with a short, thick neck. Head with many chitinous projections bearing chaetae, the number and arrangement variable by species. Eyes present, ovoid, placed anteriorly on head. Antennae inserted between eyes. Gula distinct. Mouthparts shaped as in Dorylocerus, with all palpi having a similar complement of segments. Antennae 11-segmented.

Pronotum with chitinous projections, the number and arrangement variable by species. Prosternum shaped as in Dorylocerus excisicollis and D. solea, with well-defined carina longitudinally along midline. Each elytron with well-defined carinas, the number and detailed structure of which vary by species. Mesothoracic peritremes well-defined, containing mesothoracic spiracles and closing procoxal cavities behind. Mesosternum with a long, thin, acarinate process extending to metasternum between metacoxae. Mesosternum short, metasternum long. Legs shaped as in Dorylocerus; tarsal formula 4-5-5.

Abdominal segment I membranous. Segment II represented by the tergite only. Segments III-VII each with a tergite, sternite, and 2 pairs of paratergites. Inner paratergites of segment VII reduced to small sclerites near spiracle. Spiracles on abdominal segments not conspicuously enlarged. Seg-

ment VIII represented by a tergite and sternite only. Segment IX complex, shaped as in Dorylocerus. Tergal gland reservoir beneath tergite VI. Opening to the tergal gland on the anterior border of tergite VII. Sternites III-VII with raised, chitinous projections. Tergites with raised chitinous projections, the number variable by species. Spermatheca exceedingly small and transparent. Male genitalia unknown.

KEY TO SPECIES OF DRACONULA

Lateral border of pronotum with 2 distinct indentations..... D. minuta
Lateral border of pronotum smooth and evenly indented toward the middle.... ..... D. decellei

Draconula decellei, n. sp.
Figures 2A & 3A

Most closely related to D. minuta from which it is distinguished by the shape of the pronotum, which is acarinate and bears a lesser number of projections; the lesser number of carinas on the elytra; and the sculpturing of the abdominal tergites.

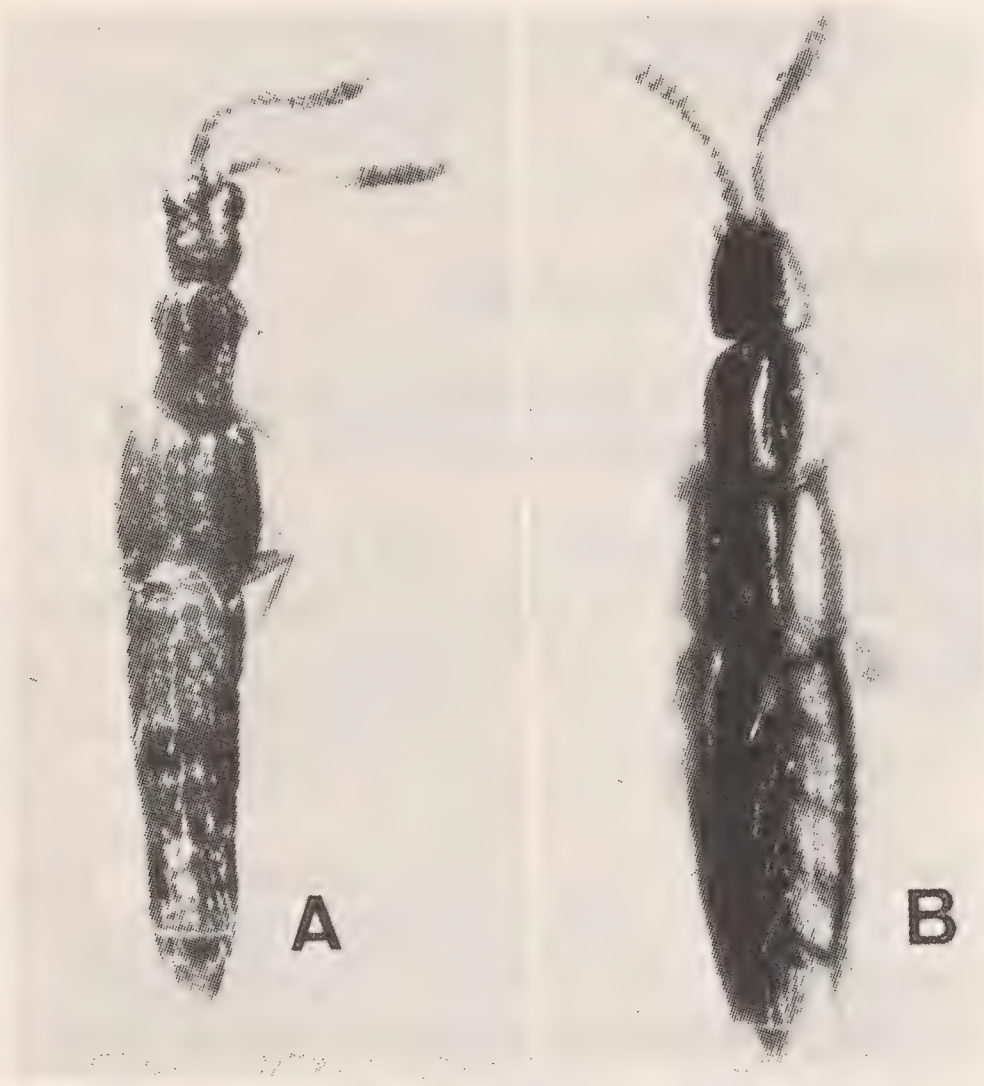

Fig. 2-- Dorsal photos to show entire beetle: A, Draconula decellei; B, Dorylobius sulcicollis Raffray.

Yellowish-brown throughout; head and pronotum a little darker; elytra much darker. Ground sculpture of head, pronotum, and elytra shagreened. Head with 14 large tubercles arranged in 4 rows, 2 dorsal and 2 lateral, the dorsal rows of five tubercles each leading anteriorly to a U-shaped upraised carina at anterior margin of head with a finely serrate edge. Anterior-most tubercles with two short chaetae, the area between the bases of the chaetae slightly depressed. All other tubercles with one chaeta. Lateral rows with two tubercles each, each tubercle with one chaeta. Pronotum acarinate; with one lateral chitinous projection on each side in the anterior portion, each followed by a row of 4 chaetae. Elytra with well-defined lateral and medial carinas with deeply depressed areas between them. Sculpture and facies as in Fig. 2A; abdominal tergites II-VIII as in Fig. 3A; with projections from posterior borders and macrochaetotaxy as shown and with raised areas. In addition, the dorsal edges of sternites III-VII are raised, forming lateral carinas which have their highest point anteriorly and taper down posteriorly;

sternites II-VI also have projections each bearing 2 chaetae, as shown in Fig. 3A. Genitalia unknown.

Measurements--Head length, 0.30; head width, 0.20; pronotum length, 0.38; elytra length, 0.27. Number measured, 1.

Holotype--1♂ No. 13630, Zaire Republic, Yangambi, nr. Stanleyville, 16. XI. 1955, Coll. J. Décelle, with Dorylus (Anomma) kohli Wasmann. In the collection of the Musée Royal de l'Afrique Centrale, Tervuren.

Genus Dorylocerus Wasmann (Reconstituted)

Dorylocerus Wasmann 1904: 627; Seevers 1965: 298; Kistner 1968: 275
Dorylopora Wasmann 1904: 628; Wasmann 1915: 203, (revision and key); Fenyes 1920: 334; Seevers 1965: 298-9 (listing plus a catalog of species); Kistner 1966: 342 (revision); Kistner 1968: 275 (key to genera); 279 (new records). New Synonymy.
Dorylocosta Cameron 1930: 416 (proposed as a subgenus); Kistner 1966: 342 (synonymy to Dorylopora).

The key given on p. (43) will serve to distinguish this genus from all others. The description as given by Kistner (1966) for Dorylopora still holds except that the pronotum shape is still more variable as the genus now includes 2 species with campanulate pronota.

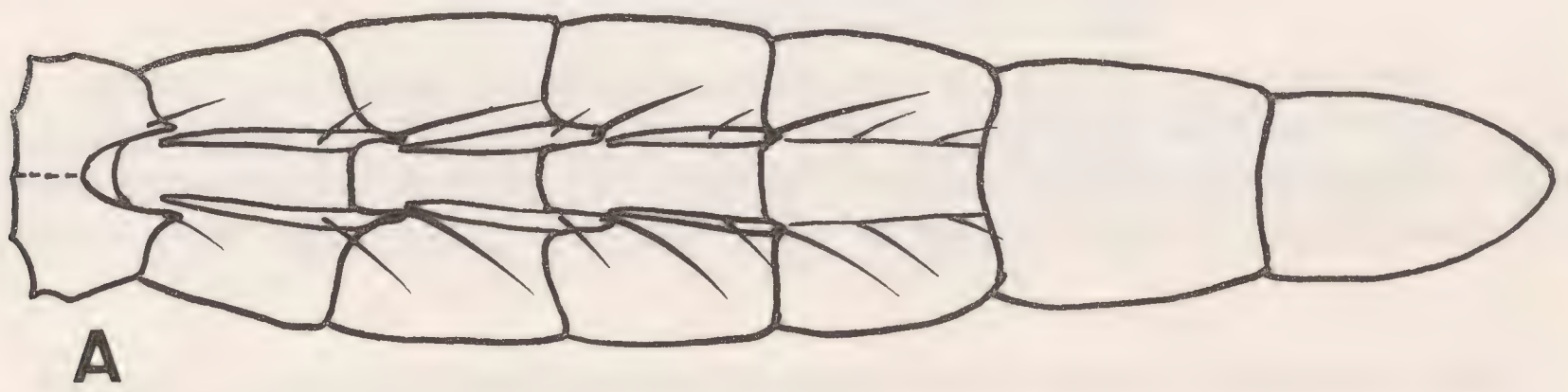

Fig. 3--Abdominal tergites II-VIII: A, Draconula decellei; B, Dorylocerus carinata.

KEY TO THE SPECIES GROUPS OF DORYLOCERUS

1 Posterior borders of abdominal tergites with no notches or indentations of any kind.....2
Posterior borders of abdominal tergites with at least one notch and/or projections.....3
2 (1) Lateral borders of pronotum smooth, not notched or indented in any way

.....kohli group
Lateral border of pronotum with shallow indentation as the overall shape pronotum is campanulate..... fossulatus group
3 (1) Posterior borders of some abdominal tergites notched or indented, but with no projections..... 4
Posterior borders of some abdominal tergites notched, indented, and with raised projections..... excisicollis group
4 (3) Lateral borders of pronotum indented.....congolensis group
Lateral borders of pronotum smooth..... costata group

Dorylocerus kohli group

Species of this group can be separated from each other reliably only by the shape of the spermathecae. Since this shape was not used for the numerical analysis, 4 of the species had perfect correlations (see Fig. 1). Four species belong to this group: D. afer, D. kohli, D. morio, and D. nigra. We have no new records of these species.

Dorylocerus fossulatus group

This species group has but 1 species, Dorylocerus fossulatus, which is still known only from the type specimen.

Dorylocerus excisicollis group

This species group contains the species included in the key below. It was formerly split into the abdominalis group, the excisicollis group, and the alzadae group but the way they cluster out (Fig. 1) indicates that these should all be in 1 group if the group is going to be equivalent to the other species groups.

KEY TO SPECIES OF THE DORYLOCERUS EXISICOLLIS GROUP

1 Lateral borders of pronotum smooth, not notched 2
Lateral borders of pronotum notched or indented.....4
2 (1) Pronotum elongate and campanulate..... D. carinata
Pronotum evenly rounded at lateral border..... 3
3 (2) Abdominal tergites II-VI with indentations and projections...abdominalis
Abdominal tergites II-IV with indentations and projections.....carlislei
4 (1) Abdominal tergites II-IV with notches; tergites II-III with projections also; tergite V without notches or projections 5
Abdominal tergites II-V with notches and projections..... 6
5 (4) Abdominal tergite IV with a notch and posterior projections..excisicollis
Abdominal tergite IV with a feeble notch but no posterior projections.... .....solea
6 (4) Raised portions of tergites III-VI all completely separated.....alzadae
Raised portions of tergites IV and V not separated distinctly into 2 rows 7
7 (6) Raised areas of tergite II joining anteriorly.....kalongeana
Raised areas of tergite II not joining anteriorly.....minor

We have new records for 1 of the species and 1 new species:

Dorylocerus carinata, new species
Figure 3B

Distinguished from all other species, including D. abdominalis to which it is most closely related, by the shape of the pronotum and the sculpture of the abdominal tergites.

Reddish brown throughout. Ground sculpture of the head, pronotum, and elytra punctate. Head with a median longitudinal and 2 lateral furrows which are delineated by well-defined carinas which are smooth; anterior border of the vertex delineated by a toothed carina. Pronotum somewhat campanulate, with a median and 2 lateral furrows, all delineated by carinas. Lateral borders of the pronotum smooth, not notched. Elytra with raised carinas at lateral and median borders and depressed areas between them. Sculpture and facies similar to that of D. carlislei. Abdominal tergites II-VIII as shown in Fig. 3B, tergites III-V with medial notches surrounded by posterior projections from the posterior border, also with raised portions on tergites II-VI as shown by stippling in the figure.

Measurements--Pronotum length, 0.360; elytra length, 0.355. Number measured, 1.

Holotype--Male, No. 14535, Zambia, Mbala, 20.V.1970, in an emigration column of Dorylus (Anomma) wilverthi Emery, Nest No. 169, Coll. J. R. Clover, D. H., A. C., A. H. and K. M. C. Kistner. In the collection of Kistner.

Dorylocerus minor (Eichelbaum)

New Records: 6, Rhodesia, Mt. Selinda, 14-15.IV.1970, from the central parts and ends of raiding columns of Dorylus (Anomma) nigricans ssp. burmeisteri var. molestus (Gerst) Mayr., nest #166 and 168, Coll. J. R. Clover, D. H. and A. C. Kistner, and R. Boulton.

Dorylocerus congolensis group

While the width of the pronotal furrow is wider in D. ivoiriensis than in D. congolensis, the species are reliably separated only by the shapes of the spermathecae.

We have a new record of the following:

Dorylocerus congolensis (Kistner)

New Record: 1, Uganda, 30 mi ex Hoima-Ft. Portal, 5 July 1970, from the central part of a raiding column of D. (A.) nigricans ssp. burmeisteri var. rubellus (Santschi), nest no. 185, Coll. D. H., A. C., A. H., and K. M. C. Kistner.

Dorylocerus costata group

1. Abdominal tergites II and III only with notches.....D. pseudocostata
   Abdominal tergites II, III, and IV with notches.....2
2. Head with only a median groove.....D. costata
   Head with a median groove defined by raised carinas..... D. fletcheri

Dorylocerus costata (Wasmann)

Additional bibliography: Dorylopora costata, Levasseur 1968: 57 (Central African Republic, La Moboke).

New Records: 4, Uganda, 30 mi ex Hoima - Ft. Portal, 5 July 1970, from the central part of a raiding column of D. (A.) nigricans ssp. burmeisteri var. rubellus (Santschi), nest no. 185, Coll. D. H., A. C., A. H., and K. M. C. Kistner; 4, Kenya, Masai Mara Game Reserve, at Keekorok, 26 June, 1970, from the central part of a raiding column of D. (A.) nigricans ssp. burmeisteri var. molestus (Gerst.) Mayr, nest no. 184, Coll. D. H., A. C., A. H., and K. M. C. Kistner; 2, Zambia, Mbala (Abercorn), 18-19 May 1970, ex emigration column of D. (A.) wilverthi Em., nest no. 169, Coll. J. R. Clover, D. H., A. C., A. H., and K. M. C. Kistner.

Dorylocerus fletcheri (Kistner)

New Records: 6, Rhodesia, Mt. Selinda, 15 April 1970, from the central parts and end of a raiding column of D. (A.) nigricans ssp. burmeisteri var. molestus (Gerst.) Mayr, Nest No. 168, Coll. J. R. Clover, D. H. and A. C. Kistner and R. Boulton.

Rodylopora attenuata Kistner

New Record: 1, Uganda, Kisubi forest near Entebbe, 14 July 1970, from the central part of a raiding column of D. (A.) wilverthi Emery, Nest No. 186 Coll. D. H., A. C., A. H. and K. M. C. Kistner.

BIOLOGY OF THE COMPLEX

Food habits: Observations were presented by Kistner (1966) that showed that Dorylocerus were scavengers since they were seen picking up small bits of dropped booty on the ant columns and they were also seen inside the skeletons of dead driver ants in the debris piles. Examination of sectioned specimens of D. costata, D. nigra, and D. minor has revealed that the gut is full of particulate food whereas the crops of integrated myrmecophiles such as Typhloponemys sp. and Dorylomimus kohli contain no evidence of particulate food but have special adaptations for the absorption of liquid food that is fed to them by the ants.

Social biology: Kistner (1966) showed that most species of Dorylocerus are not well integrated into the ant society. Those species that are better integrated exhibit more ridges on their bodies than those which are not integrated. We have recently completed a gland survey of D. costata, D. nigra, and D. minor which revealed a general lack of glands throughout the body. Small maxillary glands were present and small gland cells were associated with a small reservoir of the tergal defense gland under abdominal tergites VI and VII. Even hypodermal gland cells of type 1 (lubricating) and type 2 (exudatory) (see Kistner and Pasteels 1969) are scarse in species of the Dorylocerus complex. Since many type 2 cells and specialized glands are normally present in integrated termitophiles (Pasteels 1968) and myrmecophiles (Hölldobler 1970), the absence of large glands or clusters of gland cells supports the idea that they are not well integrated into the society.

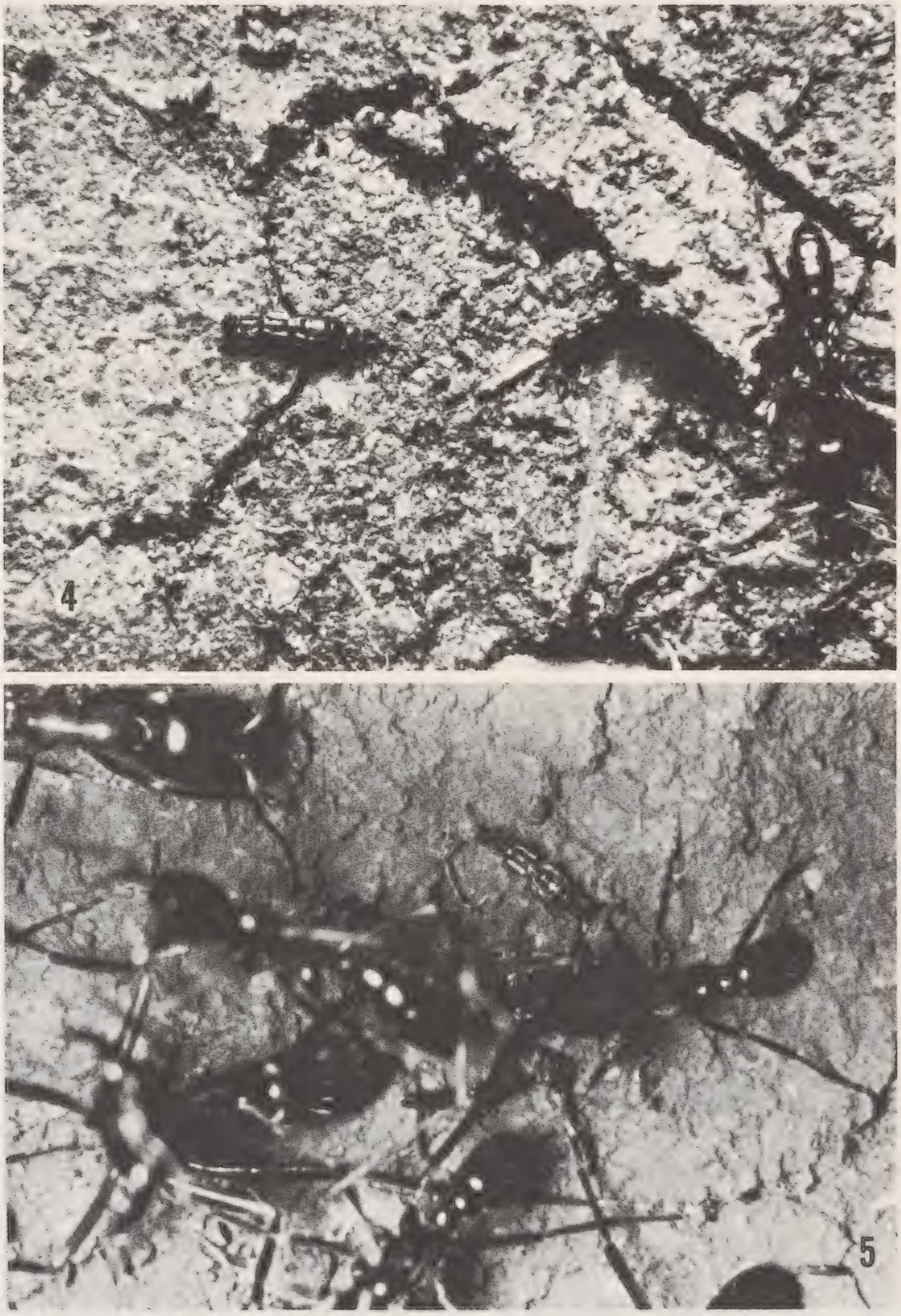

Fig. 4-5--4, Dorylocerus alzadae in a Driver ant column with the activity on an extremely low ebb. 5, D. alzadae in a column where the ant activity is more rapid. In this instance, the myrmecophile is avoiding the sentinnel workers. Both photographed in the field at Karen, Kenya in the columns of D. (A.) nigricans ssp. burmeisteri var. molestus (Gerst.) Mayr.

All of the species observed are adapted to the ant colony in that they follow the trails and adapt to the ants by avoiding areas of intense ant activity. When they travel in highly active parts of the trail, they make their way through the small pieces of dirt which the ants spread along their trails. Photographs of their positions in the columns can be seen in Fig. 4, and 5. Fig. 6 shows how they follow the trail at the end of raiding or emigration after most ants have already passed. The presence of the species of Dorylocerus in both raiding and emigration columns indicates that they follow emigrations from 1 nest to another. They would fit the behavioral criteria of generalized species as developed by Akre and Rettenmeyer (1966) for the guests of New World army ants. Their behavior fits all of their criteria except item 9 (attack adult ants but usually kill only injured or weak workers). They also do not flex their abdomens.

Evolution: The phenogram of the species of the Dorylocerus complex (Fig. 1) gives what we consider to be the most probable evolutionary sequence of the group with the most primitive species at the top of the diagram. The evolutionary trend is to increase the length of 1 or 2 pairs of carinas which run from the head posteriorly over the pronotum and elytra and continue on towards the tip of the abdomen. These ridges on the abdomen arise in 1 of 2 ways. Either they start out as a single, medial upraised area which later splits into 2 upraised lines as in Dorylocerus or they begin as 2 rows of macrochaetae which enlarge, become more heavily sclerotized and eventually become 2 ridges as in Rodylopora and Draconula. Both processes seem to be

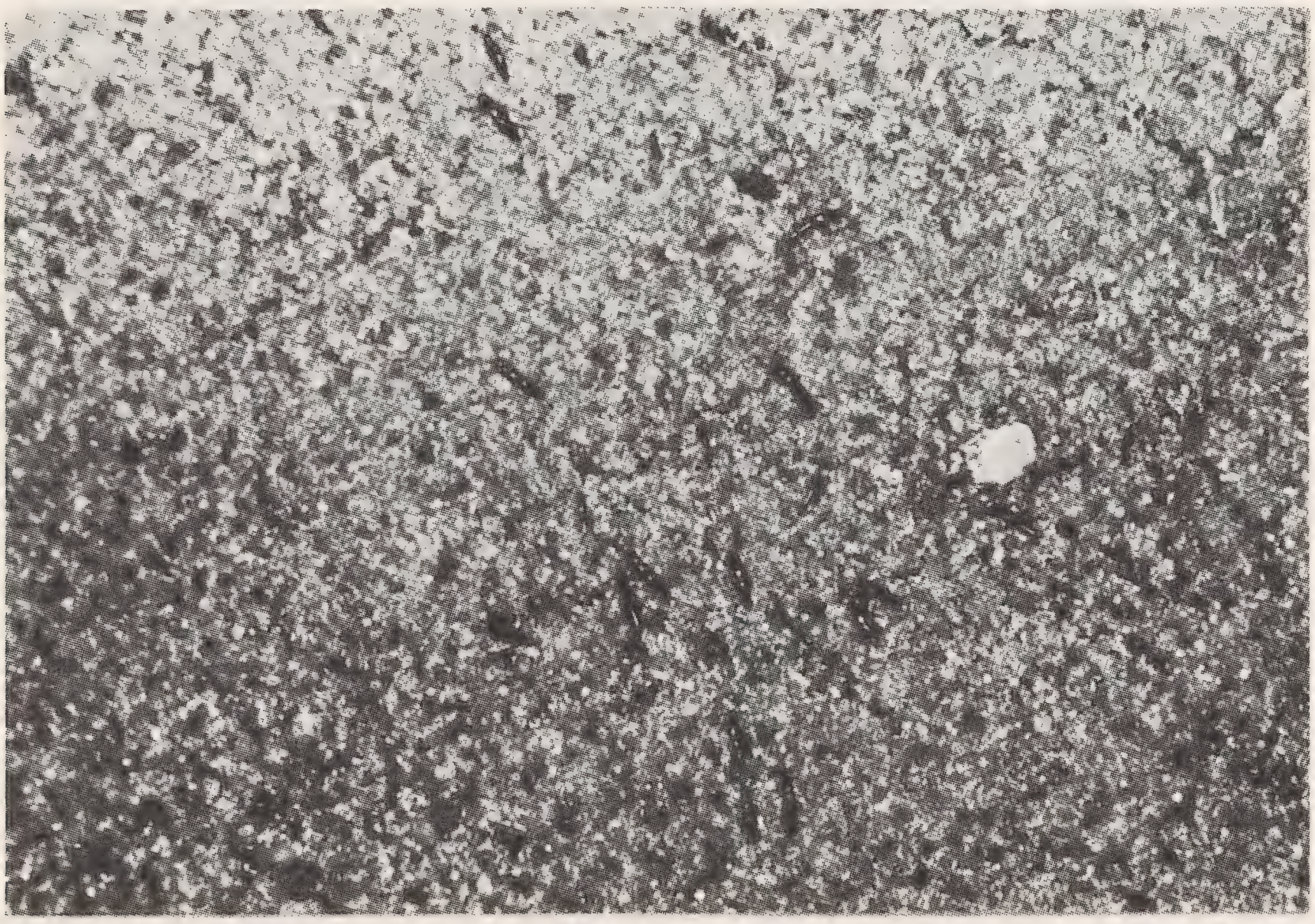

Fig. 6--After the end of raiding, numerous myrmecophiles of the tribe Deremini follow the scent trail back to the nest. Photographed in the Ivory Coast at Adiopodoumé in a trail of D. (A.) nigricans ssp. arcens (Emery)

operating in Fossulopora. The separation of the carinas is accentuated by the medial indentations which are the precursors of notches, and the projections from the posterior borders of the tergites, like the macrochaetae, serve to functionally extend the carinas from one segment to the next.

Kistner's (1966) integration data supports this view. Those species which come closest to having 2 ridges running the length of the dorsal side of the body generally are the most highly integrated. While the presence of black macrochaetae may be characteristic of the nonintegrated forms of Deremini, the development of macrochaetae may be 1 of the first steps in the evolution of carinas which results in better integration and a less hostile or possibly better protected relationship with the doryline host.

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